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Herb layer extinction debt in highly fragmented temperate forests – Completely paid after 160 years?

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ABSTRACT

The time-delayed extinction of plant species following habitat fragmentation is a well-known phenomenon in ecology. The length of the relaxation time until this ‘extinction debt’ is paid (i.e., until extinctions cease) depends on the ecosystem, species group and extent of fragmentation. Studies of grassland ecosystems have revealed that plant extirpations after fragmentation can occur rapidly when the degree of fragmentation is high. Studies of extinction debt in highly fragmented forests, however, are lacking. In this study, we evaluated the existence of an extinction debt in the Prignitz, Brandenburg, Germany, where 94% of the semi-natural forests have vanished since 1780. We surveyed the herb-layer species of 104 forest patches and fitted species richness as a function of the historical and present-day patch configurations. Models including the present-day habitat area and connectivity explained the present day species richness better than models including historical patch-configuration variables. There was no significant effect of the historical habitat area on the present day species richness. However, the effect of historical patch connectivity on the richness of forest specialists with short-distance dispersal potential was significant when excluding present-day habitat area from the models and habitat quality and heterogeneity were used as covariables. The extinction debt has largely been paid after approximately 160 years of relaxation time which contrasts with previous studies of temperate forests that have found extinction debts persisting 120–225 years after fragmentation. We demonstrate that extinction debts in temperate forests may be paid off more rapidly if the degree of fragmentation is high.

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1. Introduction

Habitat destruction and fragmentation are among the most important threats to biodiversity (Sala et al., 2000; Sax and Gaines, 2003). Although the most dramatic land-cover changes in Central Europe occurred centuries ago (especially when forests that had been more or less continuous were cut for agriculture (Darby, 1956)), there are several indications that historical land-cover changes still affect present-day species richness and community composition (Kuussaari et al., 2009). Land-cover changes can cause a time-delayed loss of species in ecological communities, which is known by the term ‘extinction debt’ (‘ED’) (Tilman et al., 1994). Given that species richness was in equilibrium before the habitat destruction event, species will eventually go extinct until the species richness reaches a new quasi-equilibrium. At this time, the ED has finally been paid. The time span from the destruction event until the ED is paid is termed the relaxation time (Kuussaari et al., 2009). Determinations of the magnitudes of an

ED and the detection of the processes that influence the magnitudes of ED are important tasks in ecology (Sutherland et al., 2013).

ED has been detected for various species groups and habitats at several spatial scales (Dullinger et al., 2012 (mountain plants); Lira et al., 2012 (small mammals); Brudvig and Damschen, 2011 (pine woodlands); Kuussaari et al., 2009 (review, listing 32 papers where an ED was found)). However, to date, only a few studies have been published for plants of temperate deciduous forests (Paltto et al., 2006; Piessens and Hermy, 2006 (in parts); Vellend et al., 2006). This paucity of studies is surprising because forest herbs are often clonal and are able to persist without sexual reproduction for many decades (Inghe and Tamm, 1985; Cain and Damman, 1997). Thus, a delay in changes in species richness in response to habitat fragmentation could be particularly pronounced in forest ecosystems.

For grassland plants, there are studies with conflicting results. Several authors have found strong evidence for the existence of an ED following habitat fragmentation (Lindborg and Eriksson, 2004; Piqueray et al., 2011), while others did not find any ED (Adriaens et al., 2006; Cousins et al., 2007; Oster et al., 2007). In

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a meta-study, Cousins (2009) noted that, in grassland studies that verified an ED, patches had retained greater than 10% of the target habitat, whereas no evidence for an ED was observed in studies in which patches retained less than 10% ('highly transformed landscape').

For plant communities of temperate deciduous forests, Paltto et al. (2006) (Sweden), Piessens and Hermy (2006) (Belgium) and Vellend et al. (2006) (UK and Belgium) have verified occurrences of an ED. In these studies, the forest covers decreased moderately by 26% in approximately 120 years (Paltto et al., 2006) and by approximately 75% in approximately 210–225 years (Piessens and Hermy, 2006; Vellend et al., 2006). However, there are many regions in Central Europe where the extent of forest area loss was substantially higher (Honnay et al., 1998; Graae, 2000, see also De Frenne et al., 2011). To date, it remains unknown as to whether or not and for how long an ED exists in such highly transformed landscapes. Our objective was to investigate ED in a region where forest area loss was greater than 94% over approximately 200 years. The answers to the questions of whether the ED has been paid or not have broad implications for conservation (Kuussaari et al., 2009; Wearn et al., 2012; Vellend and Kharouba, 2013). In scenarios with an enduring ED, conservation actions can focus on stopping or slowing down extinction processes. If there is no ED, other conservation actions may be more appropriate.

Many studies on ED use historical and present-day patch configuration to model present-day species richness (Kuussaari et al., 2009). However, species richness also depends on the habitat quality and habitat heterogeneity (Honday et al., 1999; Dumortier et al., 2002; Wulf and Kolk, 2014). The omission of these environmental factors may lead to false conclusions: A weak, but true habitat-loss-induced ED may remain undetected, or a non-existent ED may be erroneously confirmed although in fact correlations of patch configuration with environmental factors are the reason for significant results. Here, we aim to study the effects of including environmental variables when quantifying the ED.

Species do not respond to land-use changes in the same way. Several studies have revealed that forest specialists are prone to fragmentation effects (Dupre and Ehrlén, 2002; Kolb and Diekmann, 2004; Jamoneau et al., 2011; Rodríguez-Loinaz et al., 2012) and are overall more dependent on patch configuration than generalists (Dupre and Ehrlén, 2002; Kimberley et al., 2014). Specialists often have slow metapopulation dynamics, i.e. a high persistence and limited dispersal abilities, which may support delayed extinctions (Vellend et al., 2006; Hylander and Ehrlén, 2013). The analysis of trait-defined groups that represent species with slow metapopulation dynamics can give further knowledge about which specialists contribute most to an ED. A precondition is that the considered trait attributes make species respond to the spatial configuration of habitats because only then such species can constitute an ED induced by area loss and fragmentation. It has been shown that in forest ecosystems clonal species, species with low numbers of seeds per ramet and species with a short-distance dispersal potential are especially dependent on patch configuration and that such species also have low rates of colonization and a high level of persistence (Dupre and Ehrlén, 2002; Kolb and Diekmann, 2005; Kimberley et al., 2014).

Hence, we hypothesize that (a) the historical habitat area and degree of patch connectivity are better predictors for present-day species richness than present-day habitat area and patch connectivity and, in consequence, that the ED has not been paid; (b) forest specialists contribute more to an ED than generalists; (c) specialists with an extensive clonal growth, a low seed production and a short distance dispersal potential are most highly influenced by the historical patch configuration.

2. Material and methods

2.1. Study area

Our study was conducted in the Prignitz region (4217 km², 52°42'N–53°23'N, 11°15'E–12°43'E), which is located in the western portion of the federal state of Brandenburg, North-Eastern Germany (Fig. 1).

The region has an overall flat terrain with elevations ranging from 10 to 150 meters locally and is mainly subject to intensive agricultural land use. The primary soil types are Eutric Cambisols, Haplic Stagnosols and Haplic Gleysols that have developed on glaciofluvial sand deposits and loamy ground moraines (Stackebrandt et al., 1997). The mean annual temperature is 9.2 °C. The mean annual precipitation is 574 mm (DWD, 2014, Kyritz weather station). The primary forest types are large, Scots-pine (*Pinus sylvestris*)-dominated plantations, deciduous or mixed forests with oak (*Quercus robur*) and beech (*Fagus sylvatica*), and alder forests (*Alnus glutinosa*). The deciduous and mixed deciduous forests cover 18.8% of the total forested area, while the coniferous forests contribute 78.3% (see Table A.2 for the proportions of specific deciduous forest types). The area of the deciduous forest patches ranges from approximately 0.3 ha to 275 ha. The majority of the patches are less than two ha in size. These patches are often scattered within large agricultural fields.

2.2. Land-use history

Comparisons of historical and present-day patch configurations require comprehensive data on land-use history. We used the historical Schmettau map created from 1767 to 1787 at a scale of 1:50 000 (hereafter, 1780) and the Prussian government map created from 1875 to 1915 at a scale of 1:25,000 (hereafter, 1880) to derive the forest distribution during these time periods. The forest patch configuration in 1780 was used in our species richness models (sections 2.5 and 2.7). The forest distribution in 1880 was used



Fig. 1. Location of the study area in Prignitz, Brandenburg, Germany.

to identify ancient forest patches, i.e. those that have been continuously forested since 1780, and as an intermediate stage for determining the land-use changes. During the Schmettau period, the deciduous and coniferous forest stands were not clearly separated. However, [Bratring \(1804\)](#) stated that a proportion of approximately 22% of the forested land cover was coniferous forests. We used the location names provided in the Schmettau map that likely indicate coniferous tree species (e.g. 'Kien-', 'Fichten-', or 'Theerofen') and treated those areas as coniferous forests. The Prussian government map distinguished three categories of forested areas: 'deciduous forest', 'coniferous forest' and 'mixed forest'. For the area calculations, we added 50% of the area of mixed forests to the deciduous forests. To obtain the present day forest cover, we analyzed recent 1:25,000 scale topographical maps in combination with data from a statewide habitat survey ([LUA, 1995](#)). We intersected the forest distributions of the three periods using ArcGIS

10 to determine the changes in forest cover between 1780 and the present-day (see [Fig. 2](#) for separate maps for each period).

Our data indicate a massive loss of forest area between 1780 and 1880. In 1780, the total deciduous forest area was 124,293 ha. This area decreased to approximately 9375 ha by 1880 (92.4% loss). These forests were mainly converted to agricultural land and coniferous forest plantations. At present, deciduous forests cover 19,901 ha, representing a gain of 10,841 ha of deciduous forest through afforestation. However, the remaining ancient forest area was 7230 ha; thus, 1830 ha of ancient deciduous forests were lost between 1880 and the present-day. In total, the loss of ancient deciduous forests amounted to 94.2% of the 1780 area within approximately 230 years. From 1780 to the present-day, the median size of an individual deciduous forest patch decreased from 7.6 ha to 1.8 ha to 1.0 ha. In contrast, the number of patches increased from 1075 in the Schmettau period to 1459 in the Prussian period and rose to 5964 in the year 2008. Hence, the vast majority of the loss of deciduous forest area occurred during the first period examined (from 1780 to 1880), while the degree of fragmentation increased remarkably between 1880 and the present-day.

2.3. Patch selection

Forest patches that fit our study aim had to be largely ancient and deciduous (allochthonous coniferous stands rarely constitute a habitat for forest specialists). Therefore we only included patches where the majority share was deciduous. From this selection, we further only used patches whose ancient deciduous forest share was more than 33%. Moreover, we only included patch sizes from 0.5 to 25 ha into our 'patch pool' in order to keep the sample size high and the fieldwork manageable. We used a stratified random sampling for the selection of 110 ancient forest patches (out of a pool of 178 suitable ancient patches) for our field survey. As strata, we used the area of deciduous forest (five subclasses, [Table A.1](#)) and the main forest community types, based on [Hofmann and Pommer \(2005\)](#), which are connected to nutrient and water availability ([Table A.2](#)). Community types were assigned to a patch when the areal extent of the community type in the patch was at least 1000 m². This means that there could be more than one forest community type per patch. The numbers of patches in each area class ([Table A.1](#)) and the numbers of patches with a specific forest community type ([Table A.2](#)) were not evenly distributed. To ensure that less frequent forest types would be represented in the study, we calculated probability weights for each class combination and used these weights for the random sampling of patches. Six patches were omitted after fieldwork because they were either strongly affected by other land use types (cemetery, park, archaeological site) or the area was restricted and thus inaccessible. The total habitat area of the 104 remaining patches was 65 643 ha in 1780 and 561 ha in 2008 representing a total loss of 99.2%. The median of the habitat area in a patch was 742 ha in 1780 and 2.8 ha in 2008. The habitat loss within a patch ranged from 57.1% to 99.9%. The habitat loss was under 90% in only seven patches. The mean deciduous forest cover within a buffer zone of 1000 m surrounding each patch was 47.2% in 1780 and 4.6% in 2008, thus connectivity had decreased for all 104 patches.

2.4. Species richness

We recorded all vascular plant species in the herb layer (≤ 1 m, tree saplings were excluded) by walking 20-m wide transects. We surveyed the whole deciduous forest area of a patch, i.e. the transect length depended on the deciduous forest area of a patch. We included the species growing at the within-forest edges and the species at the inner patch edges, i.e., all species growing inside of

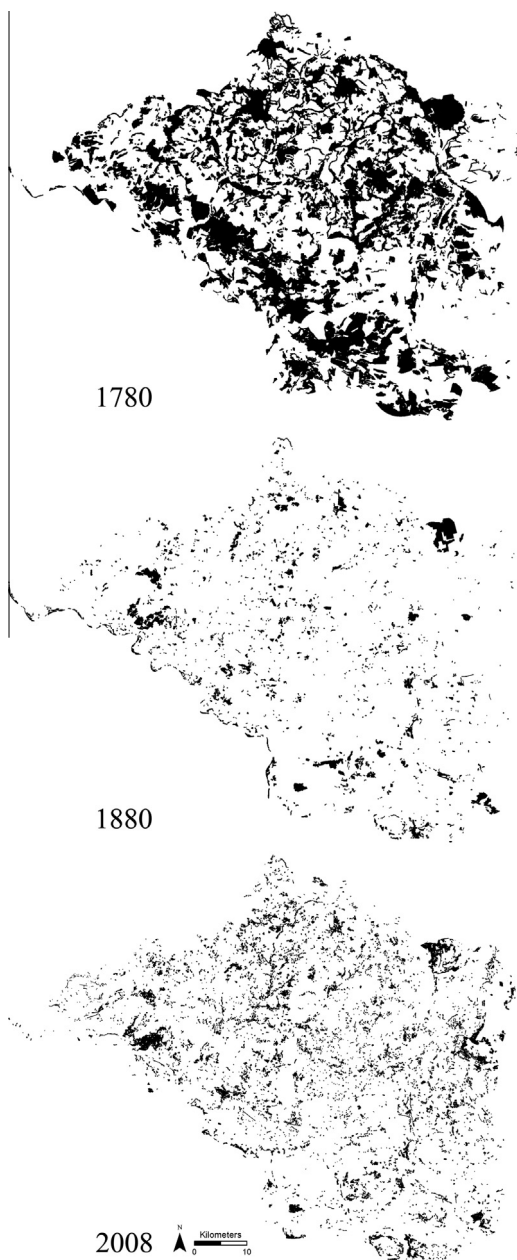


Fig. 2. Extent of deciduous forests in the Prignitz region in NW Brandenburg, Germany, in the years 1780, 1880 and 2008.

the outermost tree line. We excluded coniferous stands, clear-cut areas and areas where there was no clearly visible tree-layer. The species growing in mixed forests were included when the deciduous component was dominant. To include both spring and summer species, we performed two field campaigns, from mid-April to May 2013 and from June to August 2013, respectively.

We determined the species richness per patch for several species groups: (a) all species, (b) forest specialists, i.e., species restricted to the closed forest environment (species of category 1.1 in the list of Schmidt et al., 2011), (c) species that are not forest specialists (hereafter called 'generalists', i.e., species that grow in forests as well as in open environments (categories 2.1 and 2.2 in Schmidt et al., 2011), those that grow at forest edges (category 1.2 in Schmidt et al., 2011) and those that are not included in the list), and (d) within the specialists the trait groups of extensive clonals, species with few seeds per ramet and species with short-distance dispersal potential.

We defined extensive clonals as specialists with ≥ 2 offspring shoots per parent plant per year. The trait data was acquired from the CloPla database (Klimešová and de Bello, 2009). To identify specialists with few seeds per ramet, we used the mean number of seeds per ramet from the LEDA traitbase (Kleyer et al., 2008) and classified all specialists with a seed number below the median (<154 seeds per ramet) as specialists with few seeds per ramet. Specialists with a short-distance dispersal potential were defined as those belonging to the dispersal mode groups 1, 2 and 3 (representing species with a dispersal distance up to 15 m) from Vittoz and Engler (2007). Dispersal mode data was mainly taken from Müller-Schneider (1986) and, in addition, from Jäger and Werner (2005) and the floraweb database (Floraweb, 2014).

2.5. Present day and historical patch configuration

We performed a comparison of the present and historical patch configurations to detect the ED, e.g., Lindborg and Eriksson (2004). To characterize the present day and historical patch configurations, we employed two variables: habitat area and patch connectivity. The historical habitat area was the forest area of the patch in 1780. The present day habitat area was the area dominated by deciduous tree species, i.e., the area in which we recorded the plants in the fields. The variables were $\log(1+x)$ -transformed to obtain a more equal distribution what enables us to detect underlying patterns more clearly. We calculated the patch connectivity based on the percent of habitat area within a buffer zone of 1000 m surrounding the recorded area of the patch. For the historical connectivity, we calculated the percentage of deciduous forest area in 1780 relative to the total buffer area. For the present day connectivity, we only included the patches that contained ancient forest stands with an area of at least 1000 m². We did not consider purely post-agricultural forests because these habitats cannot be assumed to hold any source populations of forest specialists yet.

There are numerous opinions on how to calculate connectivity and on how to choose an appropriate buffer distance (Moilanen and Nieminen, 2002; Calabrese and Fagan, 2004). We choose a buffer distance of 1000 m, which is a commonly used distance for forest plant-specific studies (Kolb and Diekmann, 2004; Endels et al., 2007; Bergès et al., 2013), because most forest plants have a maximum dispersal distance that is <1000 m (Thomson et al., 2011). We did not use Hanski's incidence function model (Hanski, 1998) because Moilanen and Nieminen (2002) reported problems with using this measure for highly fragmented habitats. In our study, we compared highly fragmented (present-day) forest patches with nearly continuous (1780) forest patches. The present day and historical connectivity was $\log(1+x)$ transformed for analysis to obtain a more equally distribution of values.

2.6. Habitat quality and habitat heterogeneity

To characterize habitat quality, we collected soil samples in September 2013. Five samples (within a distance of 1 m) were collected from a sampling depth of 10 cm (after litter removal) at the most base-rich spot of each patch (following the approach of Kolb and Diekmann (2004)). The expected species richness in temperate forests is highest on base-rich sites, which are also often close to groundwater (Härdtle et al., 2003). Hence, the most base-rich portion of a patch is best suited for predictions of species richness. This spot was determined visually based on expert knowledge of the plant species' indicator values for soil chemistry (Ellenberg et al., 2001). We mixed all five soil samples from a patch together. Afterwards, we immediately weighed the samples, air-dried the samples and weighed them again to determine the soil moisture content. After sieving (2-mm mesh), the samples were analyzed for total carbon and nitrogen by the dry combustion method (ISO 10694 and ISO 13878). In addition, we calculated the C/N ratio from the percentages of total carbon and total nitrogen. We determined the contents of phosphorus and potassium per 100 g soil using the double calcium lactate method at pH 3.6, with potassium and phosphorus determined photometrically. To determine the content of calcium (-orthophosphate) per 100 g soil we used an extractant solution of ammonium acetate in combination with acetic acid and hydroxypropionic acid. We measured the magnesium content per 100 g soil by atom absorption spectrometry after extraction with a calcium chloride solution. The soil pH was determined in 0.01 M calcium chloride using a glass electrode (ISO 10390). All soil variables were log-transformed to meet assumptions of normality. To reduce the number of variables, we performed a principal component analysis with varimax rotation using the 'principal' function in the Psych R package (Revelle, 2013). The first three axes represented 84% of the total variance in soil variables. The first axis was positively correlated with soil moisture, nitrogen and carbon supply ('moisture-axis'). The second axis was positively correlated with pH and calcium availability ('soil pH-axis'). The third axis was positively correlated with the phosphorus and potassium ('P-availability-axis') contents of the soils (Table A.3).

We evaluated habitat heterogeneity by assessing four variables: subpatch diversity, geological diversity, topographical heterogeneity and edge effect. The subpatch diversity reflects the man-made diversity of the patches. In the field, we differentiated each patch into homogeneous subpatches based on the composition and structure of the woody layers. We then used the area of each subpatch to calculate the Shannon diversity per patch. For geological diversity, we aggregated information from geological maps into twelve substrate types (Table A.4). We determined the substrate-type area per patch and calculated the Shannon diversity per patch. To measure topographical heterogeneity, we determined the range in elevation based on a digital elevation model (resolution 25 m; height accuracy ± 2 m). The range values were $\log(1+x)$ -transformed for analysis to obtain a more equally distribution of values for a better interpretation of the results. Lastly, the edge effect variable was defined as the total edge length (including both the outer edge of the habitat area and within-patch edges (e.g., forest tracks or aisles)) divided by the perimeter of a theoretical circular patch constructed with the same habitat area. We used this calculation to decouple the edge length from the habitat area of the patches. The variable edge effect was log-transformed before analysis to approximate a symmetric distribution.

2.7. Data analysis

First, we conducted a correlation analysis to investigate the relationships between the historical and present-day patch

configuration variables and the habitat quality and heterogeneity variables. Next, we compared statistical models to explain species richness that included the historical habitat area and connectivity against models that included the present-day habitat area and connectivity. We assumed that, if the historical model does explain the variation in present day species richness better than the present day model, then the herb layer plant community in our forest patches exhibits an ED. If the present day model performs better, we assume that the ED has been paid. For modeling, we first considered generalized linear models (GLM) with a Poisson error distribution. Subsequently, we checked for overdispersion and, in that case, we instead used a negative binomial model (GLM-NB) (following Lindén and Mäntyniemi (2011)). The GLM-NB models were fitted using the R-function “glm.nb” from the MASS package (Venables and Ripley, 2002).

In a first step, we fitted models without the addition of the habitat quality and habitat heterogeneity variables. Then, we looked for the best combination of habitat quality and habitat heterogeneity variables to explain species richness. For this purpose, we fitted models for all possible variable combinations and selected the model that contained only significant predictors and had the lowest AIC-value. This was our basic model. We then added the variables for the historical habitat area and historical patch connectivity to the basic model to determine the influence of the historical patch configuration in combination with present day habitat quality and heterogeneity variables on species numbers (historical model). For the present day model, we added the variables for the present-day habitat area and patch connectivity to the basic model. We compared the AIC-values of the historical and present day models and assumed that the model with the lowest AIC-value best explained species richness.

Finally, to assess the combined effects of the historical and the present day area and connectivity, we created another model that included the significant patch configuration variables in addition with the habitat quality and habitat heterogeneity variables of both the historical model and the present-day model (combined model). These three models (historical, present day and combined) were compared to the basic model by performing likelihood-ratio tests to determine if there were significant differences. For the negative binomial models, we used the adapted likelihood-ratio test ‘anova.negbin’ from the MASS package (Venables and Ripley, 2002). We created models for the total number of species in the herb layer, for the numbers of forest specialists and generalists, and for each of the specialists groups. All predictor variables were standardized to a mean = 0 and an SD = 1 to facilitate the interpretation of the parameter estimates (Schielzeth, 2010). All of the analysis steps were performed using R, version 3.0.2 (R Core Team, 2013).

3. Results

We identified 374 herb-layer plant species in the 104 forest patches, with a mean number of 71.8 per patch (SD = 30.5; range 25–150). Sixty-five (17.3%) of these species were forest specialists (16.9 per patch; SD = 8.0; range 1–35), while 309 (82.7%) were generalists (55 per patch; SD = 25.1; range 20–120).

The correlation analysis (Table 1) revealed only marginal correlations of the habitat quality and heterogeneity variables with the historical patch configuration variables. Historical patch connectivity correlated weakly and negatively with topographical heterogeneity. Correlations between present-day patch configuration variables and habitat quality and heterogeneity were more distinct, especially for present-day habitat area.

The models that included the present-day patch configuration variables generally explained species richness better than the models including the historical patch configuration variables

(Table 2). For both, the historical and the present-day models, the inclusion of habitat quality and –heterogeneity variables led to lower AIC-values, i.e. to models with a better fit. The AIC-values of the historical models did not differ significantly from those of the basic models.

The models revealed only a weak relationship between the historical patch configuration and the present day species richness (Table 3). In the models without the habitat quality and heterogeneity variables we found no significant effects of the historical patch connectivity and area on present-day species richness. When including the additional habitat quality and heterogeneity variables the results indicate a significant effect of the historical patch connectivity on the richness of specialist species. The historical patch connectivity also had a significant effect on the richness of specialists with short-distance dispersal potential. There was no significant effect of the historical habitat area on any species richness variable. The AIC-values of the combined models for specialists and short-dispersing specialists were only slightly lower than the AIC-values of the model including the present-day patch configuration alone (Table 2). In these models, the historical patch connectivity was no longer a significant predictor variable. Including historical patch connectivity also did not alter the significance of the other patch variables either (Table 3). All of the present-day models indicated a strong influence of habitat area on species richness (Table 3). The present-day patch connectivity was not significant in any model. Furthermore, there was a strong influence of habitat quality on species richness. Species richness increased with increasing soil moisture and nitrogen availability (PCA-axis 1) and decreasing P-availability (PCA-axis 3), but was not influenced by soil pH (PCA-axis 2). In contrast, the richness of generalists was only dependent on P-availability. Habitat heterogeneity in terms of the subpatch diversity, geological diversity and topographical heterogeneity was only significant in the historical and basic models, with few exceptions. Habitat heterogeneity in terms of the edge effect was more influential. In particular, the edge effect significantly influenced the richness of generalists and was also influential in the model for all herb species.

4. Discussion

4.1. Present-day patch configuration predicts species richness better than historical patch configuration

Our study on examining the ED in highly fragmented forests revealed contrary results to studies conducted in less fragmented areas from Paltto et al. (2006), Piessens and Hermy (2006) and Vellend et al. (2006). The present-day species richness was largely determined by the present-day patch area, in combination with habitat quality. Hence, our data does not support the hypothesis of an ED for herb layer plant species after approximately 160 years of relaxation time. Our results are in line with studies that have examined highly fragmented grasslands (Berglund and Jonsson, 2005; Bagaria et al., 2012) and with the review study of Cousins (2009). Cousins (2009) noted that, in grassland studies that reported an ED, the patches still retained greater than 10% of the original target habitat. In contrast, the studies conducted in highly transformed landscapes did not report any evidence of an ED. The fragmentation of forest patches in our study region was very dramatic. Our investigated patches retained only approximately 0.8% of the area that was present in 1780 and the degree of connectivity had decreased considerably. Across our entire study region, 94.2% of the ancient forest area had been transformed. The vast majority of the deciduous forest area was lost by 1850 (Wulf et al., 2010). Hence, the relaxation time in our study area was approximately 160 years. This time span is within those of other ED studies that have examined temperate forests who are approximately

Table 1

Pearson correlation between patch configuration variables and habitat quality and heterogeneity variables.

	Area 1780	Connectivity 1780	Area 2008	Connectivity 2008
Edge effect	0.03	0.01	0.58***	0.05
Moisture	0.09	0.07	−0.10	0.12
Soil pH	−0.01	0.01	0.12	0.22*
P-Availability	0.07	0.03	−0.41***	−0.01
Subpatch-diversity	0.04	0.06	0.52***	−0.01
Substrate-diversity	0.10	0.05	0.31***	0.01
Topographical heterogeneity	−0.20	−0.33***	0.49***	−0.32***

* Significance: $0.01 < P \leq 0.05$.*** Significance: $P \leq 0.001$.**Table 2**

AIC-values of models of species richness as a function of the historical and the present day patch configurations. Models that included patch configuration were tested against the model without patch configuration by performing a likelihood-ratio-test.

Species richness of	Config. only 1780	Config. only 2008	Env. without config.	Env. with config. 1780	Env. with config. 2008	Env. with conn. 1780, area 2008
All herbs	1000.0	895.1	912.1	913.6 ^{n.s.}	867.8***	
Herb specialists	733.9	652.3	670.9	670.1 ^{n.s.}	638.0***	637.2***
Herb generalists	954.3	873.9	880.9	882.5 ^{n.s.}	849.2***	
Few seeds per ramet	598.7	540.4	555.6	556.8 ^{n.s.}	535.5***	
Short-distance dispersal	633.2	568.7	587.9	586.8 ^{n.s.}	563.0***	562.2***
Extensive clonals	576.2	501.3	473.1	474.8 ^{n.s.}	451.4***	

Config. = patch configuration, Env. = habitat quality and heterogeneity variables.

*** Significance: $P \leq 0.001$.

120 years in [Paltto et al. \(2006\)](#) and approximately 210–225 years in [Piessens and Hermly \(2006\)](#) and [Vellend et al. \(2006\)](#). We conclude that the main reason for the complete payment of the ED is the truly massive loss of habitat and the reduced level of connectivity rather than a long relaxation time.

4.2. Historical patch connectivity affects forest-specialist richness

The species richness of all herbs and of the generalists was not dependent on the historical patch configuration, but we detected an effect of the historical patch connectivity on the species richness of the specialists. We only found this effect in the models that included the additional habitat quality and heterogeneity variables. The effect was also marginal in the combined models, i.e. when historical connectivity was included to the model with the present-day habitat area ([Table 3](#)). These results suggest that the inclusion of the additional habitat quality and heterogeneity variables had an influence on the significance, i.e. the strength of the relationship of historical patch connectivity with present-day species richness. When looking at the correlation analysis ([Table 1](#)) it can be seen that correlations of the habitat quality and heterogeneity variables with the historical patch connectivity are weak to non-existent. However, there was one variable, the topographical heterogeneity, that showed a weak, though significant negative correlation with historical patch connectivity. Unfortunately, we cannot explain why the historical patch connectivity should be smaller in regions with a high topographical heterogeneity. One could imagine that in regions with a high topographical heterogeneity soils are less suitable for agriculture. According to our maps, this was not the case for our study area. To test whether topographical heterogeneity is the crucial variable that lets historical patch connectivity become significant, we fitted a model for specialist species richness without topographical heterogeneity, but all other variables. In this case the historical connectivity was no more significant ([Table A.5](#)). However, we also fitted models omitting other, less correlated variables (e.g. soil moisture) and in several of these models the historical connectivity also turned

non-significant ([Table A.5](#)). Thus, we assume that the main reason for the significance of historical patch connectivity is that the inclusion of the habitat quality and heterogeneity variables reduces the amount of unexplained variation in the models, which means that the true, though weak effects of historical connectivity become more important relative to the total unexplained variation. Although the reason for the weak correlation between topographical heterogeneity and historical patch connectivity remains obscure and the effects of correlations in general seem to be small in our study, our study demonstrates that historical effects on species richness may be masked by environmental patch attributes. Considering environmental conditions in the examination of extinction debts should therefore be standard in future studies.

Our results suggest that forest specialists contribute more to the ED than generalists because the richness of forest specialists was still dependent on the historical patch configuration (although only in one model combination), while the richness of generalists was not. The results also support the well-known influence of patch configuration on forest specialists, in contrast to generalists ([Rodríguez-Loinaz et al., 2012](#); [Kuussaari et al., 2009](#); [Petit et al., 2004](#)). However, because the ED has largely been paid now the specific contributions of the specialists and generalists to the ED cannot be quantified anymore.

We detected a significant relationship between specialist species richness and historical patch connectivity, but not historical habitat area. It is unlikely that there was never an ED associated with habitat loss. In the present-day models, habitat area was the most important factor for explaining species richness, and the amount of habitat loss was very high. We expect that the ED associated with habitat loss was quickly paid off. Connectivity has not dropped as dramatically as habitat area and the majority of habitat fragmentation occurred after the reduction in forest area. A massive area of habitat had been lost by 1850, while the increase in the number of patches (i.e., the degree of fragmentation) primarily occurred from 1880 to 2013. [Bommarco et al. \(2014\)](#) noted the importance of historical connectivity over a historical area with respect to delayed extinctions. These authors reported a connection

Table 3

Results of the regression models of forest herb species richness in 2013 against patch configurations (in 1780 and 2008), habitat quality and habitat heterogeneity. The first row of each group provides the model results without the inclusion of patch configuration variables. The second row provides the model with the historical patch configuration variables only. The third row provides the model with the present day variables only. The fourth row includes the model with the historical patch configuration and additional habitat quality and heterogeneity variables. The fifth row includes models with present day patch configuration and additional habitat quality and heterogeneity variables. The sixth row includes the model with the present day habitat area and the historical patch connectivity. For each model, the standardized regression coefficients and significance are shown.

Species richness of	Area	Con-nectivity	Moisture	Soil pH	P-avail.	Subpatch diversity	Geological diversity	Topog. heterogen.	Edge effect
All herbs	x	x	0.08 [*]	x	−0.15 ^{***}	0.08 ⁺	x	x	0.22 ^{***}
1780	−0.03 ^{n.s.}	0.05 ^{n.s.}	x	x	x	x	x	x	x
2008	0.34 ^{***}	0.02 ^{n.s.}	x	x	x	x	x	x	x
1780	−0.02 ^{n.s.}	0.05 ^{n.s.}	0.07 ⁺	x	−0.15 ^{***}	0.08 ⁺	x	x	0.23 ^{***}
2008	0.23 ^{***}	0.03 ^{n.s.}	0.06 ⁺	x	−0.08 ^{**}	0.02 ^{n.s.}	x	x	0.13 ^{***}
Herb specialists	x	x	0.18 ^{***}	x	−0.21 ^{***}	0.11 ⁺	0.07 ⁺	0.07 ⁺	0.11 ^{**}
1780	−0.02 ^{n.s.}	0.06 ^{n.s.}	x	x	x	x	x	x	x
2008	0.37 ^{***}	0.00 ^{n.s.}	x	x	x	x	x	x	x
1780	−0.03 ^{n.s.}	0.09 ⁺	0.18 ^{***}	x	−0.21 ^{***}	0.09 ⁺	0.08 ⁺	0.11 ^{**}	0.10 ^{**}
2008	0.29 ^{***}	−0.01 ^{n.s.}	0.17 ^{***}	x	−0.13 ^{**}	0.04 ^{n.s.}	0.04 ^{n.s.}	−0.00 ^{n.s.}	0.01 ^{n.s.}
Conn. 1780, area 2008	0.27 ^{***}	0.03 ^{n.s.}	0.16 ^{***}	x	−0.13 ^{**}	0.06 ^{n.s.}	0.05 ^{n.s.}	0.03 ^{n.s.}	0.01 ^{n.s.}
Herb generalists	x	x	x	x	−0.11 ^{**}	x	x	x	0.28 ^{***}
1780	−0.03 ^{n.s.}	0.05 ^{n.s.}	x	x	x	x	x	x	x
2008	0.33 ^{***}	0.03 ^{n.s.}	x	x	x	x	x	x	x
1780	−0.02 ^{n.s.}	0.06 ^{n.s.}	x	x	−0.11 ^{**}	x	x	x	0.28 ^{***}
2008	0.21 ^{***}	0.04 ^{n.s.}	x	x	−0.05 ⁺	x	x	x	0.17 ^{***}
Few seeds per ramet	x	x	0.19 ^{***}	x	−0.22 ^{***}	0.10 ⁺	0.09 ⁺	0.14 ^{**}	x
1780	−0.05 ^{n.s.}	0.04 ^{n.s.}	x	x	x	x	x	x	x
2008	0.36 ^{***}	−0.01 ^{n.s.}	x	x	x	x	x	x	x
1780	−0.04 ^{n.s.}	0.09 ^{n.s.}	0.18 ^{***}	x	−0.22 ^{***}	0.09 ^{n.s.}	0.09 ⁺	0.09 ^{***}	x
2008	0.26 ^{***}	0.00 ^{n.s.}	0.15 ^{**}	x	−0.13 ⁺	0.04 ^{n.s.}	0.05 ^{n.s.}	0.05 ^{n.s.}	x
Short distance dispersal	x	x	0.20 ^{***}	x	−0.21 ^{***}	0.12 ⁺	0.10 ⁺	0.15 ^{**}	x
1780	−0.03 ^{n.s.}	0.06 ^{n.s.}	x	x	x	x	x	x	x
2008	0.40 ^{***}	−0.02 ^{n.s.}	x	x	x	x	x	x	x
1780	−0.04 ^{n.s.}	0.12 ⁺	0.19 ^{***}	x	−0.22 ^{***}	0.10 ⁺	0.10 ⁺	0.19 ^{***}	x
2008	0.30 ^{***}	−0.03 ^{n.s.}	0.16 ^{**}	x	−0.12 ⁺	0.06 ^{n.s.}	0.05 ^{n.s.}	0.04 ^{n.s.}	x
Conn. 1780, area 2008	0.28 ^{***}	0.04 ^{n.s.}	0.15 ^{**}	x	−0.12 ⁺	0.05 ^{n.s.}	0.05 ^{n.s.}	0.07 ^{n.s.}	x
Extensive clonals	x	x	0.22 ^{***}	x	−0.21 ^{***}	0.09 ⁺	0.08 ⁺	0.08 ⁺	0.10 ⁺
1780	−0.00 ^{n.s.}	0.05 ^{n.s.}	x	x	x	x	x	x	x
2008	0.36 ^{***}	0.01 ^{n.s.}	x	x	x	x	x	x	x
1780	−0.01 ^{n.s.}	0.08 ^{n.s.}	0.22 ^{***}	x	−0.22 ^{***}	0.07 ^{n.s.}	0.08 ⁺	0.12 ^{**}	0.09 ⁺
2008	0.28 ^{***}	−0.00 ^{n.s.}	0.21 ^{***}	x	−0.14 ^{**}	0.04 ^{n.s.}	0.05 ^{n.s.}	0.02 ^{n.s.}	0.00 ^{n.s.}

x = Parameter not in model.

⁺ Significance: $0.01 < P \leq 0.05$.

^{**} Significance: $0.001 < P \leq 0.01$.

^{***} Significance: $P \leq 0.001$.

between the richness of grassland species and the level of historical connectivity, but not the area of the historical habitat. Nevertheless, the determination of the actual importance of fragmentation vs. area loss for ED remains an open question. Unfortunately, it was not possible to extend our study to a region with either a lower amount of area loss or a higher degree of connectivity. Such a comparison could provide more detail concerning the relationships of losses of connectivity and area to species extinctions in deciduous forests.

4.3. Extinction debt in forest-specialist groups

The present-day models always explained the present-day species richness of the specialists groups better than the historical models. Nevertheless, the historical connectivity influenced the richness of specialists with a short-distance dispersal potential (at least in the models that did not include present-day habitat area). This result partly confirms our hypothesis concerning the contribution of trait groups to the ED and is in accordance with the results of Vellend et al. (2006). However, the authors included species with short distance dispersal potential to a broader group of species with “slow metapopulation dynamics” which also includes other traits (see Verheyen et al. (2004) for details). For the groups of specialists with extensive clonal growth or few seeds per ramet, we did not observe the hypothesized relationship

between species richness and historical patch configuration. In the literature, persistence traits are seen as crucial to experiencing delayed extinctions (Hylander and Ehrlén, 2013). It has been shown that clonals are more sensitive to forest area loss than to connectivity (Lindborg et al., 2012). As discussed above (Sections 4.1 and 4.2), area loss was very high; thus, probably the delay for the extinction of clonals was shorter than the delay for species with short-distance dispersal potential and many clonals vanished rapidly after habitat destruction. The same rapid extinction may be true for specialists with few seeds per ramet because according to Saar et al. (2012) this trait influences both, the dispersal abilities and persistence abilities of a species. Species with few seeds have often large seeds that may enhance the persistence of a small population that is not connected to others, because species with large seeds are more competitive in (within-patch) recruitment and do cope better with temporal poor conditions after germination (Lonnberg and Eriksson, 2013; Leishman, 2003).

4.4. Implications for forest conservation

Our study demonstrates that, even in a stable environment such as that of forests, an ED can be completely paid within 160 years of relaxation time if the loss of area is extremely high. These findings demonstrate the urgency for conservation actions with respect to ED following forest fragmentation. Currently, the species richness

of the ancient forest remnants in the Prignitz region is in a state of equilibrium with the present day patch configuration. We could thus conclude that any conservation actions are superfluous. This would be too hasty of a conclusion though. We were surprised to find that the present day-patch connectivity played no role in determining species richness. However, in many other studies examining extinction debt, there was also no reported effect of present-day connectivity but was an effect of historical connectivity (e.g., Lindborg and Eriksson, 2004; Bommarco et al., 2014). If the richness of forest specialists in a patch does not benefit from the surrounding ancient forest cover (and thus other populations of forest specialists), we must assume that the metapopulation functioning has been disrupted (Jamoneau et al., 2012). If metapopulation functioning is disrupted, environmental changes can more easily lead to local extinctions (Honnay et al., 2005). Species are also unable to recolonize patches, and there are no source populations for the colonization of recently established forest patches. For forest specialists, especially those with a low dispersal potential, it will require a long time (if ever) before new populations eventually emerge (Butaye et al., 2001). In colonization processes, patch isolation is more crucial than area loss in hampering colonization of new areas (Peterken and Game, 1984). Increasing connectivity would thus largely increase the chances of species colonization in post-agricultural forests and of recolonizations in ancient forests. However, the benefits from increasing connectivity require a long time before they are realized and an ED may already be paid by the time conservation actions are finally effective. Hence, we also stress the need for active introductions of forest specialists to gain more time for conservation actions to take effect.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.12.004>.

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